24. The Skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower Neopterygian Fishes.

By C. Tate Regan, M.A., F.R.S., F.Z.S., Keeper of Zoology in the British Museum (Natural History).

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(Text-figures 1–8.)

Although a detailed and well-illustrated account of the skeleton of *Lepidosteus* was given by Agassiz in 1833 (Poissons Fossiles, vol. ii.), the nomenclature makes his description very difficult for a present-day student to follow, and it has been ignored by most modern authors. In his memoir on the development of the skull of *Lepidosteus osseus* (Phil. Trans. 1882), Parker has given a description of the skull of the adult fish which is in some respects less complete and less accurate than that of Agassiz. More recently Collinge (Proc. Birmingham Phil. Soc. viii. 1893) and Allis (Internat. Monatsb. Anat. Physiol. xxi. 1905) have studied *Lepidosteus* especially in relation to the sensory canal system. *Amia* is much better known than *Lepidosteus*, but a proper comparison of these two genera has never been made.

I propose, therefore, to describe the skeleton of *Lepidosteus*, to compare it with that of *Amia*, to discuss the systematic position of these genera, and to put forward my views as to the origin and evolution of the group to which they belong.

I have examined skeletons of *Lepidosteus platystomus*, *L. osseus*, and *L. tristoechus*; all three species are essentially similar in structure, differing from each other mainly in the shape of the bones and the number of segments of the maxillary, due to the fact that in *L. osseus* the snout is longer and narrower and in *L. tristoechus* shorter and broader than in *L. platystomus*. The nature of these differences will be seen on comparing the accompanying figures (text-fig. 1).

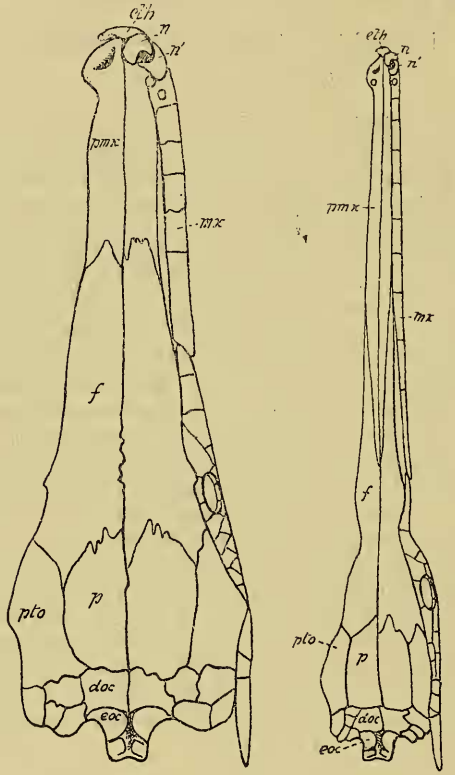
Skeleton of *Lepidosteus platystomus*.

Cranium (text-fig. 2).—The skull is elongate, narrowed forward, depressed, with the upper surface flattish anteriorly and convex posteriorly. It is well ossified, but a considerable part of the otic region remains cartilaginous, and there is a large median ethmoidal cartilage running the whole length of the rostrum.

On the upper surface a transverse series of 6 dermo-occipital plates is rigidly united to the parietals, pterotics, and epiotics, and the small, simple post-temporal is very firmly attached to the dermo-occipitals, epiotic, and pterotic. Parietals, pterotics, and

frontals are normally developed. Anteriorly there is a small dermal ethmoid, and paired nasals and adnasals cover the olfactory sacs, which lie in concavities of the præmaxillaries, above the dentigerous margin of the latter. The præmaxillaries run backwards to below the frontals, expanding on the upper surface of the snout to form a pair of rugose plates (ethmo-nasals

Text-figure 1.



A. B.

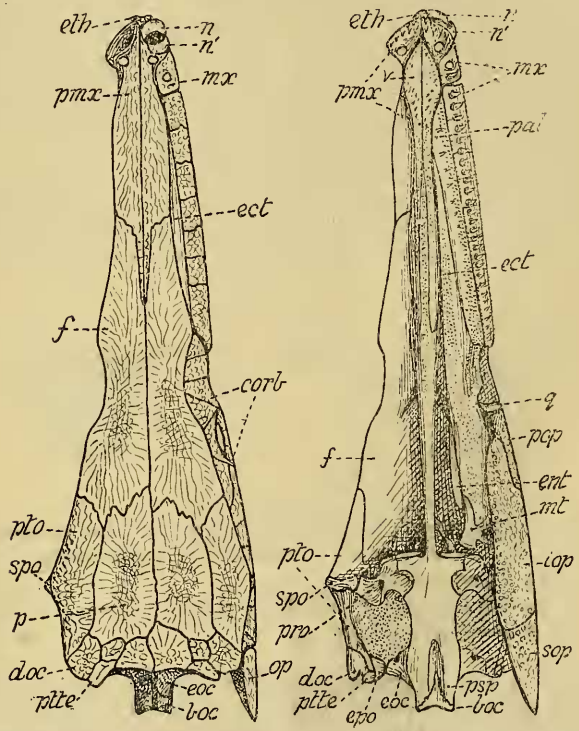
Upper surface of skull of A, *Lepidosteus tristoechus*; and B, *L. osseus*. Lettering as in text-fig. 2.

of Parker); below this they form a pair of thick-walled tubes that carry the olfactory nerves; they embrace the slender anterior portion of the rostral cartilage and are attached below to the vomers and parasphenoid (text-fig. 3).

The vomers are laminar bones attached to the lower surface of the parasphenoid and præmaxillaries; each sends back a long

process attached to the parasphenoid. In front of the orbital region the parasphenoid is V-shaped in transverse section, the ascending laminæ overlapping the præmaxillaries in front and descending laminæ of the frontals behind, with the latter

Text-figure 2.



Lepidosteus platystomus. Skull from above and from below; the pterygo-quadrate, suspensorium, opercles, etc., of one side removed.

eth. mesethmoid; *n.* nasal; *n.'* adnasal; *pmx.* præmaxillary; *mx.* maxillary; *f.* frontal; *p.* parietal; *pto.* pterotic; *spo.* sphenotic; *epo.* epiotic; *pro.* pro-otic; *doc.* dermo-occipital; *eoc.* exoccipital; *boc.* basioccipital; *ptte.* post-temporal; *psp.* parasphenoid; *v.* vomer; *pal.* palatine; *ect.* ecto-pterygoid; *ent.* entopterygoid; *mt.* metapterygoid; *q.* quadrate; *corb.* circumorbital; *op.* operculum; *sop.* suboperculum; *iop.* interoperculum; *pop.* præoperculum.

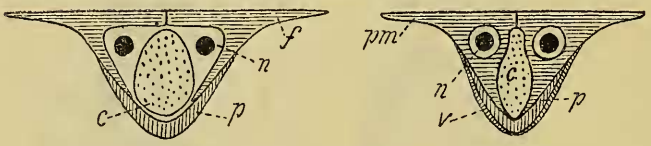
enclosing a chamber that contains the posterior part of the rostral cartilage. This does not completely fill the chamber, but on each side there is a channel for the passage of the olfactory nerves (text-fig. 3).

Behind the orbital region the parasphenoid expands, the anterior edge of each wing forming a transverse condyle for articulation with the metapterygoid. Parker's researches show that these condyles originate as separate ossifications in cartilage, and he terms them alisphenoids, but in the adult fish they are completely ankylosed with the parasphenoid.

The true alisphenoids were not seen by Parker; they are well developed and separate; they meet the pro-otics behind and are in contact with the frontals above; anteriorly they join the orbitosphenoids, which converge and ankylose anteriorly to form a short vertical plate that rests on the parasphenoid; just behind this anterior plate the orbitosphenoid is pierced on each side for the passage of the olfactory nerves (text-fig. 4).

The parasphenoid condyles are continued on to the pro-otics, which intervene between the parasphenoid and the sphenotics; inner laminæ of the pro-otics meet in the middle line and form a roof for the myodome; the pterotics ossify downwards a short

Text-figure 3.



A. B.

Lepidosteus platystomus. Diagrammatic transverse sections of the snout: A, at the level of the posterior end of the maxillary; B, at the middle of the length of the præmaxillaries.

c. rostral cartilage; *f.* frontal; *n.* olfactory nerve; *p.* parasphenoid; *pm.* præmaxillary; *v.* vomer.

distance in the cartilaginous wall of the otic region, and the epiotics are well developed; there are no opisthotics. The ex-occipitals meet, and behind them upper wings of the basioccipital almost meet in the middle line, roofing the *foramen magnum*.

Circumorbitals, etc. (text-fig. 5, A).—The orbit is surrounded by a complete series of 12 circumorbital bones; these appear externally as flat plates, but internally they are strengthened by a stout circular ridge. There are 3 præorbitals, the anterior overlapping the end of the maxillary. Behind the circumorbitals the cheek is covered with a number of irregularly arranged plates.

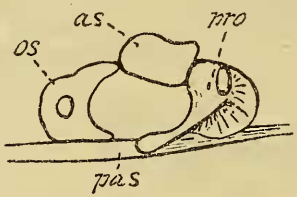
Jaws, Suspensorium, etc. (text-fig. 5).—The præmaxillaries have already been described. The maxillary is segmented into 8, the anterior piece firmly fastened to the side of the præmaxillary, the others attached to the palatine and ectopterygoid.

In the lower jaw the concave surface for the articulation of the convex condyle of the quadrate is formed by the posterior face of

an upper and the superior face of a lower ossification in Meckel's cartilage. There are well-developed angular and "supra-angular" bones, the latter curving in above the coronoid elevation. On the inner side there is posteriorly a large laminar prearticular, which ossifies through the coronoid cartilage below the anterior part of the supra-angular. In front of this a ridge of the dentary, parallel to its margin, is covered by two elongate dentigerous laminæ, the shorter anterior one entering the symphysis, the posterior ascending the coronoid elevation for a short distance external to the prearticular; on one side a small bone is intercalated at the junction of these two bones, which may be termed intra-dentaries. The prearticular and intra-dentaries are often termed collectively "splenials," but it is very improbable that any of them is the homologue of the true splenial.

The pterygo-quadrate is completely separated from the hyoid arch, and supported by it only through the articulation of the quadrate with the præoperculum. The ectopterygoid is a very long and stout bone; anteriorly it articulates with the præmaxillary above the expanded head of the vomer; the posterior

Text-figure 4.



Lepidosteus platystomus. Orbitosphenoid (*os.*), alisphenoid (*as.*), and pro-otic (*pro.*) bones; *pas.* parasphenoid. Lateral view.

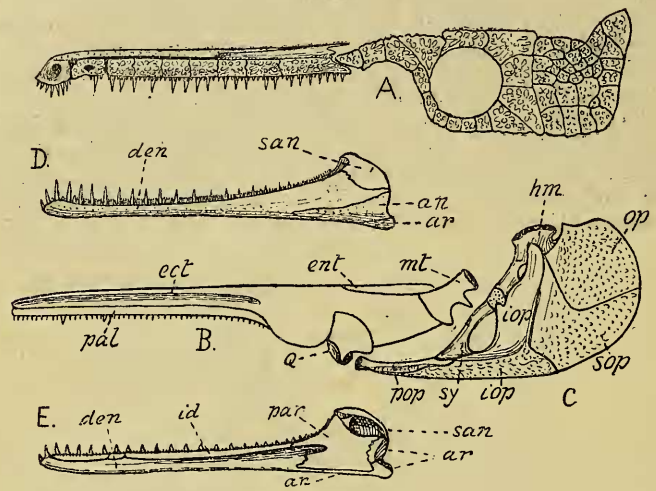
seven segments of the maxillary are firmly united to its outer face, which has a groove for their attachment; the long laminar palatine is attached to its lower surface. The entopterygoid is small, the metapterygoid bears a process for articulation with the parasphenoid and pro-otic, and the quadrate has an anterior condyle for articulation with the lower jaw and a posterior one for articulation with the anterior end of the præoperculum.

The large interoperculum is rigidly attached to the hyomandibular, symplectic, and præoperculum; the last-named is reduced to a small bone that lies above the anterior part of the interoperculum and ends in a concave facet for articulation with the quadrate. Collinge and Allis transpose the names of the præoperculum and interoperculum, on the ground that the latter is attached to the hyomandibular and transmits a branch of the sensory canal system. It may be pointed out that the interoperculum is quite normal in its relation to the suboperculum behind and the lower jaw in front, and that where it is in

contact with the præoperculum the latter lies above it. Also the analogous case of *Phractolæmus* may be quoted; in that genus the very large interoperculum transmits the sensory canal, but it is the horizontal limb of the præoperculum that is lacking, whereas in *Lepidosteus* the vertical limb has gone.

The operculum articulates with a knob on the hyomandibular, the suboperculum is well developed, and there are 3 branchiostegal rays.

Text-figure 5.



Lepidosteus platystomus.

A. Præmaxillary, maxillary, circumorbital, and cheek bones.

B. Palato-quadrate (outer view).

pal. palatine; *ect.* ectopterygoid (showing groove for attachment of maxillary); *ent.* entopterygoid; *mt.* metapterygoid; *q.* quadrate.

C. Opercular bones, etc.

hm. hyomandibular; *sy.* symplectic; *op.* operculum; *sop.* suboperculum; *iop.* interopereulum; *pop.* præoperculum.

D, E. Lower jaw, outer and inner aspects.

den. dentary; *an.* angular; *san.* supra-angular; *ar.* articulars; *par.* præarticular; *id.* intra-dentaries.

The hyoid arch comprises the hyomandibular, which articulates with the sphenotic and pterotic, the symplectic, which is firmly attached below to the præoperculum but is remote from the quadrate, the interhyal, the ceratohyal, the hypohyal, and a median basihyal. The ceratohyal has two ossifications, the hypohyal only one. The upper ossification in the ceratohyal is generally termed "epihyal;" this is certainly wrong, and I

think that there can be little doubt that the hyomandibular is the true epihyal, *i. e.* the epibranchial of the hyoid arch.

Vertebral Column.—The vertebræ are solid and opisthocœlous, with the neural arches and parapophyses ankylosed to the centra. The vertebræ number 66; from the fifty-third the vertebral column curves upwards and the vertebræ decrease in size. The neurapophyses of the first two vertebræ are short and stout; those of the succeeding vertebræ are prolonged into slender spines; the spines of each pair are in contact distally, but remain separate; the last six vertebræ have no neural spines and the last three no distinct neurapophyses. The series of supraneurals extends backwards from the first vertebra to the dorsal fin, and reappears above the end of the vertebral column, where 4 bones (epaxial supports of the caudal fin) are probably to be interpreted as belonging to it. Each supraneural is more or less expanded or even bifid proximally; the first two are short and stout, and articulate with the neurapophyses of the first two vertebræ; the rest are slender, attached to the neural spines. The ribs are expanded proximally for articulation with the distal ends of the strong transverse parapophyses. From the forty-first vertebra backwards the parapophyses become shorter and are directed downwards; their ribs also are downwardly directed, and behind the anal fin unite to form hæmal spines; the hæmal spines of the upturned vertebræ are expanded as hypurals to support the caudal fin; the hypurals are only one less in number than the upturned vertebræ, but in the specimen examined they are displaced, so that the sixtieth vertebra bears two and some of the last six vertebræ do not bear any.

Fin Skeleton.—The dorsal and anal fins are supported by a series of pterygiophores, each of which is divided into a long proximal (basal) and a short distal (radial) segment; each fin-ray is articulated to its radial. The pelvic bones are rather long and flat; they converge and slightly overlap anteriorly; only the innermost radial is well developed, the fin-rays articulating directly with the pelvic bones. The pectoral arch includes a small simple post-temporal, which is firmly united to the skull, a supra-cleithrum, and a cleithrum. The coracoid cartilage has only one ossification, the hypercoracoid (or "scapula"): there are 4 radials, 3 of which articulate with the hypercoracoid and one with the metapterygium.

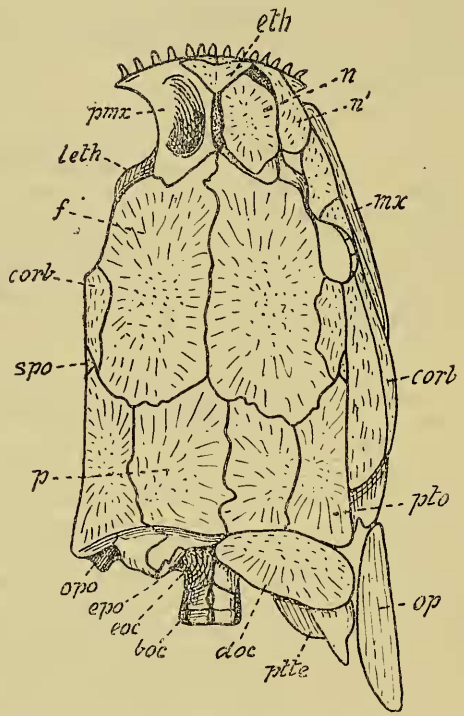
Comparison of *Lepidosteus* with *Amia*.

Cranium.—In *Amia* the orbito-rostral part of the skull is much shorter and broader than in *Lepidosteus*, and the *cavum cranii* extends forward between the orbits to the ethmoid region. On the upper surface a single pair of loose dermo-occipital plates represent the three pairs or more of *Lepidosteus*; the other bones, parietals, pterotics, frontals, præmaxillaries, nasals, adnasals, and dermal ethmoid, have precisely the same relationship to each

other as in *Lepidosteus*, differing only in form and proportions; owing to the shortness of the snout the præmaxillaries are scarcely exposed on the upper surface behind the nasals, and when the nasals and adnasals are removed it is seen that the long tubes that carry the olfactory nerves in *Lepidosteus* are represented by mere foramina.

The rostral cartilage contains paired septo-maxillary and lateral ethmoid ossifications; the vomers and parasphenoid are broad and flat, and the latter is unconnected with the frontals; the

Text-figure 6.



Amia calva. Skull from above. For comparison with text-fig. 2. Lettering as before.

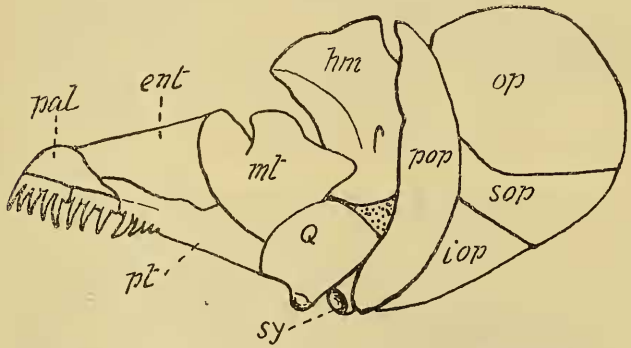
wings of the parasphenoid do not bear condyles and do not unite with the pro-otics, but extend upwards to unite by suture with the sphenotics and internally with the alisphenoids; the orbitosphenoids are paired and separate. Small paired basisphenoids are present, narrowly separated and projecting upwards in front of the pro-otics, which roof the myodome just as in *Lepidosteus*; sphenotics and epiotics are much as in *Lepidosteus*, but in addition there are well-developed opisthotics, and above them on

each side a posterior temporal fossa roofed by the epiotic and pterotic. Exoccipitals are as in *Lepidosteus*, but the upper wings of the basioccipital in that genus are represented in *Amia* by two or three pairs of bones, generally interpreted as the neural arches of centra incorporated in the basioccipital.

Circumorbitals.—In *Amia* the circumorbital series is incomplete above, and the bones are reduced in number; there is a single præorbital, two large postorbitals cover the cheek, and above them a smaller one appears at the side of the frontal as a bone of the cranial roof.

Jaws, Suspensorium, etc.—As already noted, the præmaxillaries of *Amia* have the same relation to the dermal ethmoid, nasals, adnasals and frontals, and to the olfactory sacs and nerves as in *Lepidosteus*, but the maxillaries are quite unlike those of that genus, for they are unsegmented and free; each has an inwardly

Text-figure 7.

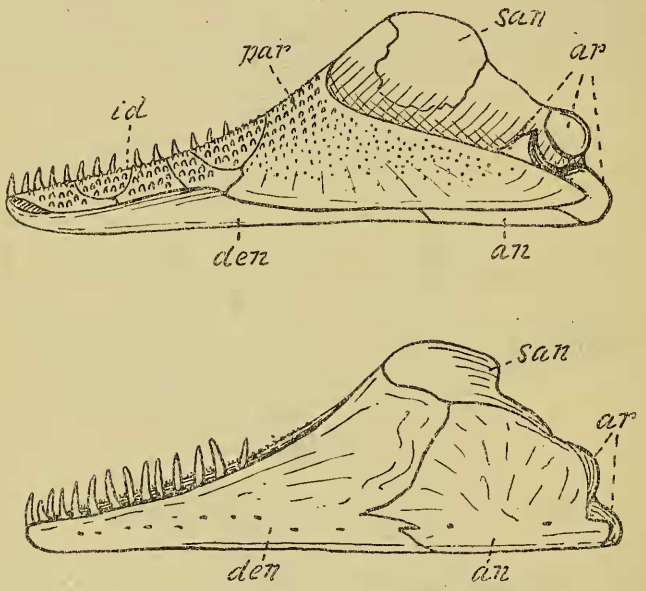


Amia calva. Pterygo-quadrate, suspensorial, and opercular bones. Lettering as in text-fig. 5.

directed articular process at the anterior end, and each carries a supplemental bone (or supramaxillary). The lower jaw of *Amia* has two endosteal bones for articulation with the quadrate as in *Lepidosteus*, but there is an additional small bone in front of the upper of these, and above them is another additional bone with a convex posterior surface for articulation with the concave anterior end of the symplectic. The dentary, angular, and supra-angular correspond to those bones in *Lepidosteus*, and, as in that genus, there is a large laminar præarticular; in front of this Allis shows two intra-dentaries, but in the skeleton I have examined, the posterior of these is represented on one side by four bones and on the other by six; also in my example the endosteal mento-Meckelian figured by Allis appears to be fused with the anterior intra-dentary.

Except that the palatine is separable into an endosteal ossification and two dentigerous laminæ, the pterygo-quadrate, hyoid, and opercular bones are the same as those of *Lepidosteus*; but they are very differently arranged, for the metapterygoid is firmly attached to the hyomandibular and the quadrate to the symplectic, the well-developed crescentic præoperculum is united to the hyomandibular and symplectic, and the interoperculum is normally developed and movable. Some authors have described a process of the metapterygoid as articulating with the pro-otic, but actually there is no such articulation, and the process,

Text-figure 8.



Amia calva. Lower jaw, inner and outer aspects.
Lettering as in text-fig. 5.

which is an intermuscular lamina directed upwards, forwards, and outwards, does not go anywhere near the otic region of the skull.

Amia has a good series of branchiostegal rays and a median gular plate. The ceratohyal has two ossifications and the hypohyal one as in *Lepidosteus*, and the branchial skeleton shows no important differences from that genus.

Vertebræ and fins.—The vertebral column of *Amia* is well known; the most important differences from *Lepidosteus* are that the vertebræ are amphicœlous, and that in most of the

caudal vertebræ each centrum is divided into a præcentrum (without arches) and a postcentrum. The terminal vertebræ, hypurals, etc., are arranged much as in *Lepidosteus*. The skeleton of the fins is as in *Lepidosteus*, except that the pectoral radials are more numerous and more than one articulates with the metapterygium; the pectoral arch differs from that of *Lepidosteus* in that the coracoid cartilage is unossified and the post-temporal is large and loosely attached, with a lower fork running to the opisthotic.

Systematic Position of *Lepidosteus* and *Amia*.

It is probable that most of the characters in which *Lepidosteus* and *Amia* agree are common to all the Holostean Ganoids (Semionotidæ, Pycnodontidæ *, Macrosemiidæ, Eugnathidæ, Amiidæ, Pachycormidæ †, Aspidorhynchidæ). Further, it is evident that the essential features which distinguish *Lepidosteus* from *Amia*, *i. e.* the characters of the jaws, suspensorium, and opercles, distinguish it also from all the others. *Lepidotus* is extremely like *Amia* in its head skeleton, except that the skull is more compressed, with the epiotics meeting above the exoccipitals and the orbitosphenoids united (*cf.* Smith Woodward, P. Z. S. 1893, and Mon. Palæontogr. Soc. 1916–1919). I am fairly certain that I can make out in this genus the symplectic articulation with the lower jaw.

The Semionotidæ, to which family *Lepidotus* belongs, first made their appearance in the Upper Permian, and are very distinct in structure from the Palæoniscidæ, the only fishes known which can be regarded as their ancestors. The typical Palæoniscids appear to have been swift-swimming predacious fishes, with a large mouth and sharp teeth. If we regard them as giving rise to the Semionotidæ, probably slow-swimming bottom-feeding fishes, with a small mouth and styliform or tritoral teeth, we can interpret many of the differences as related to a change of habits.

The change from dorsal and anal fins with numerous rays forming a close-set series to fins with the rays relatively few and spaced, each ray with its own pterygiophore, and the reduction of the muscular lobe at the base of each fin and of the radial segments of the pterygiophores, are readily understandable if the use of these fins changed from cleaving the water and withstanding strains to performing the delicate movements of a fish at rest or swimming slowly. Correlated with this modification of the dorsal and anal fins is that of the caudal, the upturned end of the

* These are aberrant in the reduction of the opercular apparatus and the arrangement of the bones of the cranial roof.

† The præmaxillaries are said to be loose and separated by an ethmoidal rostrum, but I am not satisfied that this interpretation is correct. I think that the so-called præmaxillaries may be the fractured anterior ends of the maxillaries.

tail being shortened so that the fin became terminal rather than ventral. The use of the jaws for crushing shell-fish instead of seizing fishes may account for the firm union of the præmaxillaries with the frontals. The lower jaw of the Palæoniscids appears to have consisted of the same four bones as that of *Polypterus*, namely dentary, angular, articular, and præarticular; that of the Semionotids is shorter, deeper, and stronger, and the additional articular ossifications (as seen in *Amia*) may simply be due to the increased size and complexity of its articulation, whilst the intra-dentaries may be regarded merely as plates developed to support teeth. The "supra-angular" may be an anterior bone of the outer circumorbital series which has adhered to the coronoid process, in the same way that a bone of the temporal series has become attached to the hyomandibular in *Polypterus*; and I believe that the supplemental maxillary had a similar origin. The small size of the mouth involved a change in shape and direction of the præoperculum and hyomandibular; the præoperculum, which in the Palæoniscidæ appears to have been simply a plate covering the cheek behind the circumorbitals, now became used to strengthen the suspensorium, a necessity on account of the forward position of the articulation of the lower jaw; the lower end of the elongated hyomandibular ossified as the symplectic, which may have been originally developed either, as I am inclined to think, for the articulation of the lower jaw, or perhaps only to support the quadrate and connect it with the præoperculum; the original hyomandibular ossification developed a knob for articulation with the operculum; the upper ossification in the cerato-hyal appears to have been developed for the attachment of the interhyal, which seems to be an ossified ligament. It is obvious that the character of the respiration would be greatly changed, the movements being smaller, and I think that a better regulation of these would result from the definite articulation of the operculum with the hyomandibular; moreover, the hyomandibular being now but little movable, movements of the operculum became of more importance. The interoperculum is a new bone of some interest; it would almost seem as if the suboperculum, retaining its attachment to the posterior end of the lower jaw, had been elongated and then fractured, the posterior part thus retaining its freedom of movement, whilst the anterior—the interoperculum—was overlapped by the horizontal limb of the præoperculum. Finally, one may suspect that the disappearance of the clavicles is in some way connected with the other readjustments in this region.

The Semionotidæ appear to have developed in various directions, giving rise for example to the remarkable Pycnodontidæ, which show many resemblances to our modern Plectognaths; and through the Eugnathidæ to the Amiidæ and to the Pachycormidæ, which parallel the Scombroids. The development of a large-mouthed piscivorous type appears to have taken place in two

ways. In the Eugnathidæ the cleft of the mouth extended backwards and the suspensorium became vertical or directed backwards; in these strong-swimming fishes the dorsal and anal rays have increased in number and become concentrated, and the caudal has become forked. On the other hand, in the Lepidosteidæ the snout and lower jaw have grown forward, the quadrate retaining its anterior position, and we may suppose that as the lower jaw became longer and more powerful the strain on the suspensorium was relieved by the acquirement of the articulation of the metapterygoid with the parasphenoid. Other modifications, such as the great development of the interoperculum, seem to be related to the elongation of the orbital region, which gives an increased surface for attachment of the strong mandibular muscles. In these sluggish, lurking fishes the fins remain essentially as in the Semionotidæ.

The Aspidorhynchidæ, which have sometimes been associated with the Lepidosteidæ, have none of the peculiarities of that family. An analysis of their characters shows a close agreement with the Eugnathidæ, from which they differ in the prolongation of the præmaxillaries to form a beak and the development of a præsymphysial bone in the lower jaw. Especially important is the resemblance of the symplectic to that of the Eugnathidæ and *Amia* (Smith Woodward, Monogr. Palæont. Soc. 1916–1919, p. 98, pl. xx. fig. 2).

It is well known that the Teleosteans agree with the Holostean Ganoids in the structure of the dorsal and anal fins, the absence of clavicles (infra-clavicles), and the structure of the suspensorium and opercles. But the most primitive Teleosteans (*e. g.* the Elopidæ) differ from the Holostei in several important respects, as follows:—The caudal fin is homocercal*. There are three coracoid bones (hyper-, hypo-, and meso-coracoid), whereas in *Lepidosteus* and *Amia* there is not more than one (hypercoracoid or "scapula") and the mesocoracoid bridge is cartilaginous. The pectoral radials are all inserted on the hypercoracoid and hypocoracoid, the lowest radial probably representing the metapterygium. An endochondral supraoccipital bone is present. The vomer is unpaired. The lower jaw has no "supra-angular" and no intra-dentaries, and the præarticular is reduced†. The præmaxillaries are loosely attached, remote from the frontals, and in front of the olfactory sacs.

* Regan, Ann. Mag. Nat. Hist. (8) v. 1910, p. 353.

† The current nomenclature of the Teleostean lower jaw is faulty. The bone usually called angular is the homologue of the lower articular of *Amia* and the single articular of *Polypterus*. Ridewood's "endosteal articular" is the homologue of the upper articular that articulates with the quadrate in *Lepidosteus* and *Amia*. His "ectosteal articular" is the angular, and his "sesamoid articular" in all probability the præarticular.

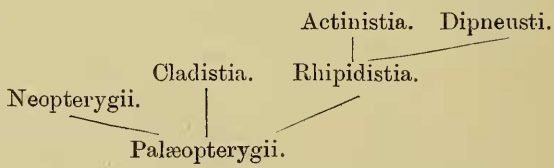
According to Ridewood (P. Z. S. 1904) the bone last named serves for the attachment of the tendon of part of the levator muscle, but it may well have persisted rather than have been developed for this purpose. In the Cyprinodonts the opisthotic is reduced to a nodule to which the lower fork of the post-temporal is attached.

If only the living forms were considered, it might be held that the Chondrostei, Holostei, and Teleostei were groups of equivalent rank. But a study of the fossils shows that this conclusion is wrong. The mesozoic Pholidophoridæ and Oligopleuridæ resemble the Holostei in the structure of the caudal fin (and in the Pholidophoridæ of their scales), but in other characters, such as the small loose præmaxillaries, the maxillary with convex oral edge and bearing two supramaxillaries*, and the absence of a "supra-angular," they show clear evidence of their relationship to the Elopidæ.

The Pholidophoridæ had minute teeth, and were probably plankton-feeders like the Herrings, which they resemble in form and in the shape of the fins. They are evidently another offshoot of the Semionotidæ, from which they differ especially in the structure of the mouth, and they lead to the Leptolepidæ and Elopidæ. These are stronger swimmers, with a deeply-forked caudal fin, in which the upper hypurals are for the first time supported by uroneurals, paired bones that replace the upturned end of the vertebral column.

The Holostei and Teleostei, therefore, are one group, for which it seems better to use the name Neopterygii, rather than to use Holostei or Teleostei in a new and extended sense; whilst the name Palæopterygii may be used to designate the group including the Palæoniscoids, Chondrostei, and Belonorhynchii.

I have long considered that the Selachians constitute a distinct class (*cf.* P. Z. S. 1906, p. 724), and if that be admitted, the main groups of the Pisces† may be termed subclasses. These are six in number—namely Palæopterygii, Neopterygii, Cladistia, Rhipidistia, Actinistia, and Dipneusti, the probable relationships of which are indicated in the following scheme :—



The Neopterygii are defined by the dorsal and anal fins with pterygiophores equal in number to the dermal rays, the absence of clavicles and of paired gulars, the presence of an interoperculum,

* It is worth noting that one supramaxillary and a supra-angular, and two supramaxillaries and no supra-angular are alternative conditions, almost suggesting that the maxillary has captured the supra-angular from the lower jaw. But it seems more likely that the supra-angular has gone, and that as the maxillary lengthened another suborbital has become attached to it.

† I exclude from the Pisces a number of Palæozoic groups of uncertain relationships, *e. g.* Arthrodira, Asterolepida, Osteostraci, etc.

and by the structure of the skull (*e.g.* typically 5 otic bones, alisphenoids and orbitosphenoids, etc.) and of the hyoid arch (a symplectic, two ossifications in the ceratohyal, etc.). This subclass contains the great majority of living fishes, and includes a large number of orders, of which the first three are :—

Order 1. Protospondyli.

Caudal fin abbreviate heterocercal. Vertebral column acentrous, or with centra variously developed*. Præmaxillaries fixed, attached to frontals and pierced for passage of olfactory nerves; maxillary free, unsegmented, usually with a supramaxillary. Lower jaw with "supra-angular," large dentigerous præarticular, and intra-dentaries. Hyoid arch and præoperculum normally developed, and symplectic firmly attached to quadrate. Only one coracoid ossification, or none ; mesocoracoid bridge cartilaginous; one or more pectoral radials inserted on metapterygium.

Principal families :—Semionotidæ, Macrosemiidæ, Eugnathidæ, Amiidæ, Pachycormidæ, Aspidorhynchidæ, Pycnodontidæ.

Order 2. Ginglymodi.

Distinguished from the preceding by the characters of the jaws, suspensorium, and opercles. Maxillary segmented, the first one or two segments attached to præmaxillary, the rest to ectopterygoid ; metapterygoids articulating with transverse facets on wings of parasphenoid ; hyoid arch free from pterygo-quadrate ; præoperculum small, its anterior end articulating with a condyle on quadrate ; interoperculum large, fixed, connecting hyomandibular with præoperculum. Vertebral centra solid, opisthocœlous.

One family, Lepidosteidæ.

Order 3. Halecostomi.

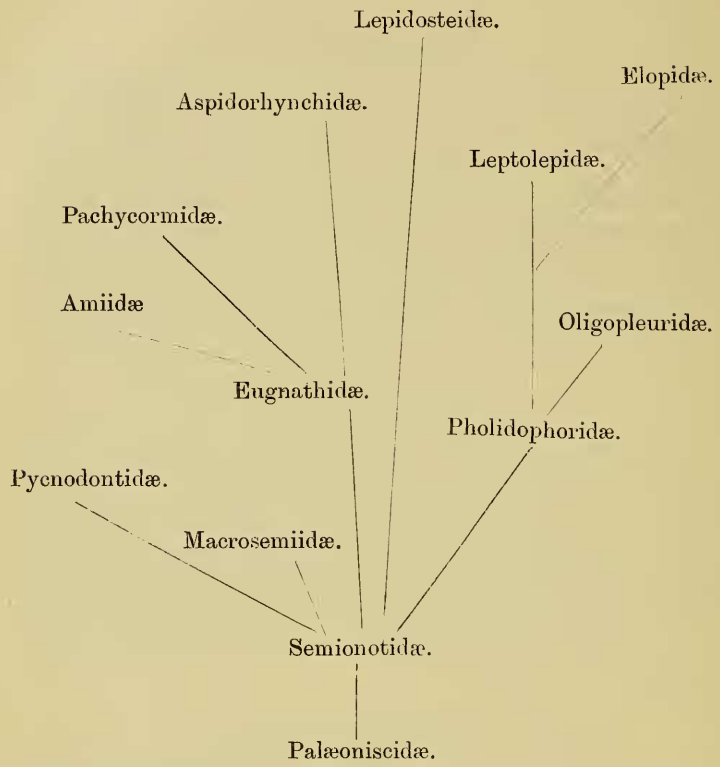
Caudal fin abbreviate heterocercal. Præmaxillaries small, loosely attached ; maxillary typically with two supramaxillaries ; lower jaw without "supra-angular" or intra-dentaries. Vertebral centra annular or amphicœlous.

Two families, Pholidophoridæ and Oligopleuridæ.

* The various conditions are :—(1) No centra; bases of arches not expanded. (This is found in all families except Amiidæ and Aspidorhynchidæ.) (2) No centra; bases of arches may form laminar expansions over the notochord (some Pycnodonts). (3) Annular or amphicœlous centra of uncertain origin; no præ- and post-centra (Aspidorhynchidæ, *Neorhombolepis*). (4) Solid outgrowths of arches may enclose notochord, forming annular centra, with præ- and post-centra in caudal region. (Some Macrosemiidæ, Eugnathidæ, and Pachycormidæ.) (5) Centra disc-like, formed by ossification of tissues surrounding notochord, enclosing bases of arches; præ- and post-centra in caudal region (Amiidæ).

The fourth Order, the Isospondyli, is distinguished from the Halecostomi by the homocercal structure of the caudal fin; it is followed by the Orders Ostariophysi, Apodes, etc.

The relationships of the families dealt with above may be expressed diagrammatically as follows:—



General Considerations.

In dealing with the origin and evolution of the lower Neopterygian Fishes I have tried to emphasize the conclusion at which I have arrived, that their differentiation has been adaptative, changes of structure being especially related to the nature of the food and the method of procuring it.

This is well illustrated by the following example:—The Semionotidæ, probably slow-swimming fishes feeding on molluscs, crustaceans, etc., appear to have been derived from the Palæoniscidæ and have themselves given rise to the Eugnathidæ,

which resemble the Palæoniscidæ in form, shape of the fins, size of the mouth, and structure of the teeth.

In comparing *Eugnathus* with *Palæoniscus*, both strong-swimming predacious fishes, it is not evident that any of the differences between them are adaptative. But these differences are due to the Semionotid ancestry of the Eugnathidæ, and there is good reason for believing that they were adaptative in origin.

The later evolution of the Neopterygian Fishes offers numbers of parallel examples; modifications persist and become the basis for further modifications.